

Second specimen of *Corriebaatar marywaltersae* from the Lower Cretaceous of Australia confirms its multituberculate affinities

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A second specimen of the Australian cimolodontan multituberculate *Corriebaatar marywaltersae* from the same locality (Flat Rocks) as the holotype and previously only known specimen, reveals far more anatomical information about the species. The new specimen, composed of most of a dentary containing a complete p4 and alveoli for the lower incisor and the lower first and second molars, exhibits a suite of features consistent with allocation of *Corriebaatar* to Cimolodonta and further confirms the presence of multituberculates on Gondwana during the Mesozoic. The revised (older) age of the Flat Rocks locality to latest Barremian (mid-Early Cretaceous) establishes *C. marywaltersae* as the oldest currently known cimolodontan. This has profound biogeographic implications for the distribution of multituberculates on Gondwana as well as globally, particularly in light of the fact that *Corriebaatar* appears to be a relatively derived member of Cimolodonta.

Key words: Mammalia, Multituberculata, Cimolodonta, Cretaceous, Gondwana, Australia.

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Introduction

Corriebaatar marywaltersae Rich, Vickers-Rich, Flannery, Kear, Cantrill, Komarower, Kool, Pickering, Trusler, Morton, van Klaveren, and Fitzgerald, 2009, was initially based on a well-preserved, little-worn, plagiulacoid lower fourth premolar (p4) attached to a very small fragment of dentary

(Figs. 1, 2). This new genus and species was placed in a new family (Corriebaataridae) and hypothesized to represent a cimolodontan multituberculate rather than a previously unrecognized mammalian lineage. Beck (2017: 335) has since suggested a third possibility, that it may be “a representative of the gondwanatherian family Ferugliotheriidae.” This specimen, NMV P216655, is the holotype and represented

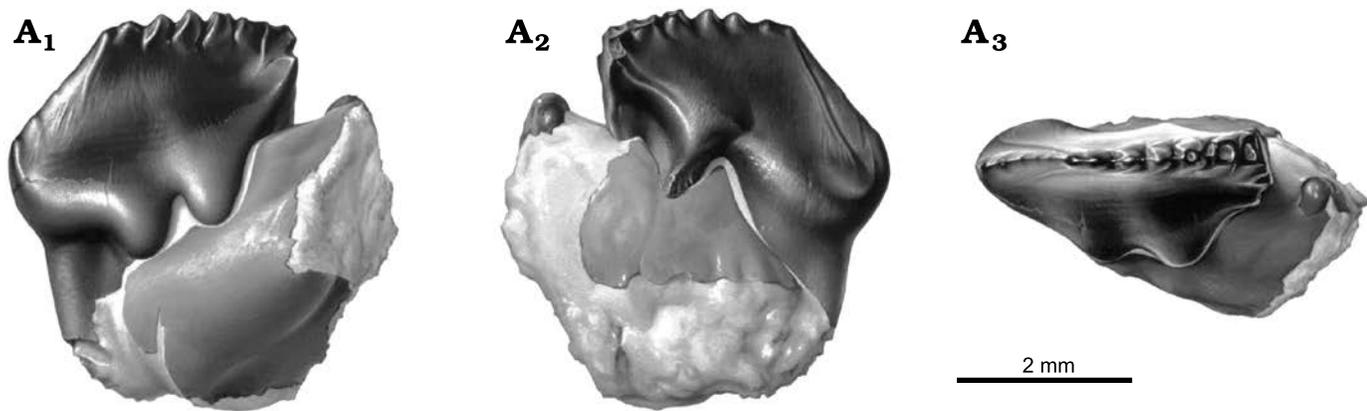


Fig. 1. Reconstruction of left p4 in dentary fragment, NMV P216655, holotype of the cimolodontan multituberculate *Corriebaatar marywaltersae* Rich, Vickers-Rich, Flannery, Kear, Cantrill, Komarow, Kool, Pickering, Trusler, Morton, van Klaveren, and Fitzgerald, 2009, Flat Rocks locality, Eumeralla Formation, Barremian, Lower Cretaceous of Victoria, Australia, in buccal (A₁), lingual (A₂), and occlusal (A₃) views. Artwork by Peter Trusler.

the only known remains of the species. It was recovered from the Flat Rocks fossil site (Victoria, Australia), now thought to be of latest Barremian (mid-Early Cretaceous) age (Wagstaff et al. 2020). The site is renowned for its collection of other early mammals, including three possible eutherians/australosphenidans (*Ausktribosphenos nyktos*, *Bishops whitmorei*, and *Kryoparvus gerriti*), and the monotreme *Teinolophos trusleri*, as well as a host of fungi, plants, paly-nomorphs, invertebrates, and other vertebrates (see overview in Poropat et al. 2018). Rich et al. (2009) suggested that NMV P216655 was the first record of Multituberculata in Australia and one of the very few records of that clade from the entire southern supercontinent of Gondwana, the other three being at the time questionable records from the Early Cretaceous of Morocco and the Late Cretaceous of Argentina and Madagascar (see reviews in Krause et al. 2017, Rougier et al. 2021, and “Biogeographic implications” section below).

A second specimen of *C. marywaltersae* was discovered in 2017 at the same Flat Rocks site as the holotype, and initially reported by Poropat et al. (2018). The new specimen, NMV P252730, consists of the horizontal ramus and anterior half of the ascending ramus of a left dentary preserving the lower incisor alveolus, a complete p4, and alveoli for the roots of m1 and m2 (Figs. 3–5). It is, therefore, much more complete than the holotype and reveals far more anatomical information about this species. Our objectives in this paper are to (i) describe and illustrate this new specimen in detail, (ii) compare it with the dentaries of a diverse array of multituberculates and other allotherian mammals in order to test the working hypothesis that *Corriebaatar* is a cimolodontan multituberculate, and (iii) assess its biogeographic significance in the context of other reported discoveries of Gondwanan multituberculates, including those made since the first specimen of *C. marywaltersae* was described in 2009.

Institutional abbreviations.—MACN-RN, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Colección Río Negro, Buenos Aires, Argentina; MPEF, Museo Paleontológico “Egidio Feruglio”, Trelew, Argentina; NMV,

Palaeontological Collection, Museums Victoria, Australia; RRBP, Rukwa Rift Basin Project, Tanzania Antiquities Unit, Dar es Salaam, Tanzania; UA, Université d’Antananarivo, Antananarivo, Madagascar.

Other abbreviations.—We follow standard convention in abbreviating tooth families as I, C, P, and M, with upper and lower case letters referring to upper and lower teeth, respectively.

Geological settings

Both specimens of *Corriebaatar marywaltersae* were recovered from sediments at the Flat Rocks fossil site on the marine shore platform in the Bunurong Marine Park to the west of Inverloch, Victoria, Australia (38°39′40±02” S, 145°40′52±03” E, World Geodetic System 1984). Previously, strata at the Flat Rocks site were assigned to the “Wonthaggi Formation” in the “Strzelecki Group” (Rich et al. 1997). However, Vandenberg et al. (2006) suggested extending application of the name Eumeralla Formation (Otway Group) from the Otway Basin to encompass equivalent deposits dominated by feldspathic sandstones in the Gippsland Basin, including those cropping out in the Flat Rocks area. Based on palynological evidence, the age of the fossil site is now considered to be latest Barremian, or mid-Early Cretaceous (Wagstaff et al. 2020). Specifically, the spore/pollen content places the Flat Rocks sediments low in the *Pilosisporites notensis* Zone. A discussion of the taphonomy of the Flat Rocks site can be found in Rich et al. (2016).

Material and methods

The partial dentary, NMV P252730, was discovered on 11 November 2017 by Wendy Jane White, who split a rock and exposed two fragments, a small anterior section (Fig. 3A₁) and a much larger posterior section (Fig. 3A₂).



Fig. 2. Left p4 in dentary fragment, NMV P216655, holotype of the cimolodontan multituberculate *Corriebaatar marywaltersae* Rich, Vickers-Rich, Flannery, Kear, Cantrill, Komarower, Kool, Pickering, Trusler, Morton, van Klaveren, and Fitzgerald, 2009, Flat Rocks locality, Eumeralla Formation, Barremian, Lower Cretaceous of Victoria, Australia; stereopairs in buccal (A₁) and lingual (A₂) views.

Due to the small size (roughly 12 mm in total length), fragile nature of the specimen, and how it was discovered (i.e., split obliquely into part and counterpart), minimal mechanical preparation was carried out; it could only safely be prepared from the medial side of the anterior section and the lateral side of the posterior section.

The two fragments were microCT-scanned separately using an Xradia Versa 520 XRM microCT at the Monash University X-ray Microscopy Facility for Imaging Geomaterials using 140 kV, 72 μ A, 10 W, $\times 0.39$ optical magnification, HE1 filter, 1.5 sec exposure, isometric voxel size = 15.167 μ m, and 1601 projections. The resulting slices were exported as 16 bit TIFs.

The image stacks were imported into Dragonfly v. 2020 (Object Research Systems Inc., Montreal, Canada). The bone region and the internal voids were masked separately. Noise due to low contrast between the bone and matrix was reduced by using the Smooth function in Dragonfly, as well as some manual editing. This depicted the voids more clearly, enabling void features (e.g., alveoli, mandibular canal) to be visually differentiated from diagenetically deformed regions. 3D meshes created from the masks were exported as object files (OBJ) and imported into the CAD software Rhinoceros 5 (Robert McNeel and Associates, Seattle, USA). Individual mesh objects were edited and exported separately.

The two 3D meshes from each of the two parts of NMV P252730 were imported into the 3D graphic design package Zbrush (Pixologic Inc, Los Angeles, USA) to undertake digital reassembly, to colour and export images for Figs. 4 and 6, and to create the 3D video of the specimen (SOM, Supplementary Online Material, available at http://app.pan.pl/SOM/app67-Rich_et_al_SOM.pdf). 3D PDFs were created using Simulation Lab Software 10.21.8 (Amman, Jordan).

Systematic palaeontology

Allotheria Marsh, 1880

Multituberculata Cope, 1884

Cimolodonta McKenna, 1975

Family Corriebaataridae Rich, Vickers-Rich, Flannery, Kear, Cantrill, Komarower, Kool, Pickering, Trusler, Morton, van Klaveren, and Fitzgerald, 2009

Genus *Corriebaatar* Rich, Vickers-Rich, Flannery, Kear, Cantrill, Komarower, Kool, Pickering, Trusler, Morton, van Klaveren, and Fitzgerald, 2009

Type species: *Corriebaatar marywaltersae* Rich, Vickers-Rich, Flannery, Kear, Cantrill, Komarower, Kool, Pickering, Trusler, Morton, van Klaveren, and Fitzgerald, 2009; monotypic, see below.

Corriebaatar marywaltersae Rich, Vickers-Rich, Flannery, Kear, Cantrill, Komarower, Kool, Pickering, Trusler, Morton, van Klaveren, and Fitzgerald, 2009

Figs. 1–6.

Holotype: NMV P216655, small fragment of left dentary bearing complete plagiulacoid p4 and mesial root of m1.

Type locality: Flat Rocks fossil site on the marine shore platform in the Bunurong Marine Park to the west of Inverloch, Victoria, Australia (38°39'40±02" S, 145°40'52±03" E, World Geodetic System 1984).

Type horizon: Eumeralla Formation (Otway Group), latest Barremian (mid-Early Cretaceous) in age (Wagstaff et al. 2020).

Stratigraphic and geographic range.—Type locality and horizon only.

Material.—Holotype and NMV P252730, horizontal ramus



Fig. 3. Partial left dentary with p4 in situ in referred specimen, NMV P252730, of the cimolodontan multituberculate *Corriebaatar marywaltersae* Rich, Vickers-Rich, Flannery, Kear, Cantrill, Komarower, Kool, Pickering, Trusler, Morton, van Klaveren, and Fitzgerald, 2009, Flat Rocks locality, Eumeralla Formation, Barremian, Lower Cretaceous of Victoria, Australia, photographed as embedded in rock matrix. Medial view of small anterior section (A₁) and lateral view of large posterior section (A₂, stereopair).

and anterior half of ascending ramus of left dentary with alveolus for root of lower incisor, complete p4 in situ, and alveoli for roots of m1 and m2, also from the type locality and horizon.

Emended diagnosis.—Differs from “plagiaulacidan” multituberculates in possessing a large, robust, laterally compressed, and erect lower incisor (all except *Glirodon*); absence of p1, p2, and p3; mesial root more robust than distal root on p4; presence of interradicular crest between mesial and distal roots of p4; absence of buccal row of cusps (or cuspules) on p4; presence of accessory roots on molars; m1 only one-half the length of p4; and m2 shorter than m1. Differs from most cimolodontans in absence of p3 and in possession of extraordinarily short buccal and lingual ridges descending from serrations along apical crest of p4. Differs from all cimolodontans in possessing two, sharply divided exodaenodont lobes (mesial and distal) on buccal aspect of p4 (incipiently developed in *Ferugliotherium*) and in long, straight buccal and lingual ridges descending ventromesially from first serration.

Description.—NMV P252730 is a left dentary fragment composed of the tooth-bearing horizontal ramus and the anterior portion of the ascending ramus (Figs. 3–5; video of specimen presented in SOM). The dentary itself is much more complete than the tiny fragment attached to the roots of p4 and the mesial root of m1 on the holotype, NMV P216655 (Rich et al. 2009: figs. 1, 2). The horizontal ramus of the new specimen reveals for the first time that the dental formula of *Corriebaatar marywaltersae* is likely 1.0.1.2, including a large, laterally compressed lower incisor, a plagiaulacid p4, and two molars. The p4 is complete in NMV P252730, whereas the lower incisor and two molars are represented only by alveoli (except for small fragments of roots inside the alveolus for the lower incisor and the mesial alveolus for m1).

The alveolus for the lower incisor is incomplete, with small portions of the rim broken away (particularly a V-shaped piece ventrolaterally), but most of it is preserved. In lateral view, the mesial (medial) side of the rim was positioned dorsal to that on the distal (lateral) side. The portions that are preserved indicate clearly that the alveolus

hosted a large, mediolaterally compressed tooth, one that was approximately 2.2 mm tall and 0.7 mm wide and therefore over three times taller than wide, although this may be exaggerated because of mediolateral compression. The alveolus extends to beneath the mesial edge of the distal root of p4 and does not taper significantly, suggesting that the root may have been ever-growing, or at least grew late into life. In dorsal view, the alveolus passed posteriorly in a plane medial to the mesial root of p4. The angle of the alveolus in lateral view suggests that the incisor was implanted at a steep angle and that the crown would have been quite erect, projecting anterodorsally at approximately 116° relative to the ventral margin of the dentary.

A short diastema is present (1.62 mm) between the lower incisor and p4 (measured as a straight line from the distal rim of the incisor alveolus to the mesial rim of the mesial alveolus of p4). In lateral view, this diastema is strongly concave dorsally, representing approximately one-third of a circle, with its mesial end being at about the same height as its distal end. There is no trace of a p3 (or alveolus for it), even as a diminutive peg-like tooth, and we therefore regard it to be absent in this taxon.

The single preserved cheektooth in NMV P252730 is strikingly similar to the equivalent tooth in the holotype, NMV 216655, and is here interpreted as the p4; the crown and root morphology of this tooth, coupled with features of the dentary, show strong resemblance to multituberculates in general and Cimolodonta in particular. We therefore assume, as a working hypothesis based on available material, that this tooth is the p4, and that the other, more mesial premolar positions have been lost in the lineage leading to *C. marywaltersae*. Although there is a slight difference in size, we have little doubt that the two specimens belong to the same species. The p4 in NMV P252730 is complete and well preserved but considerably more worn than that of the holotype, NMV P216655, indicating a more mature individual. The new specimen measures 3.62 mm long (as measured along the baseline from the apex of the mesial projection of the crown to the point where the distobuccal ledge intersects the distal margin; see Krause 1987: fig. 1) and 1.52 mm wide

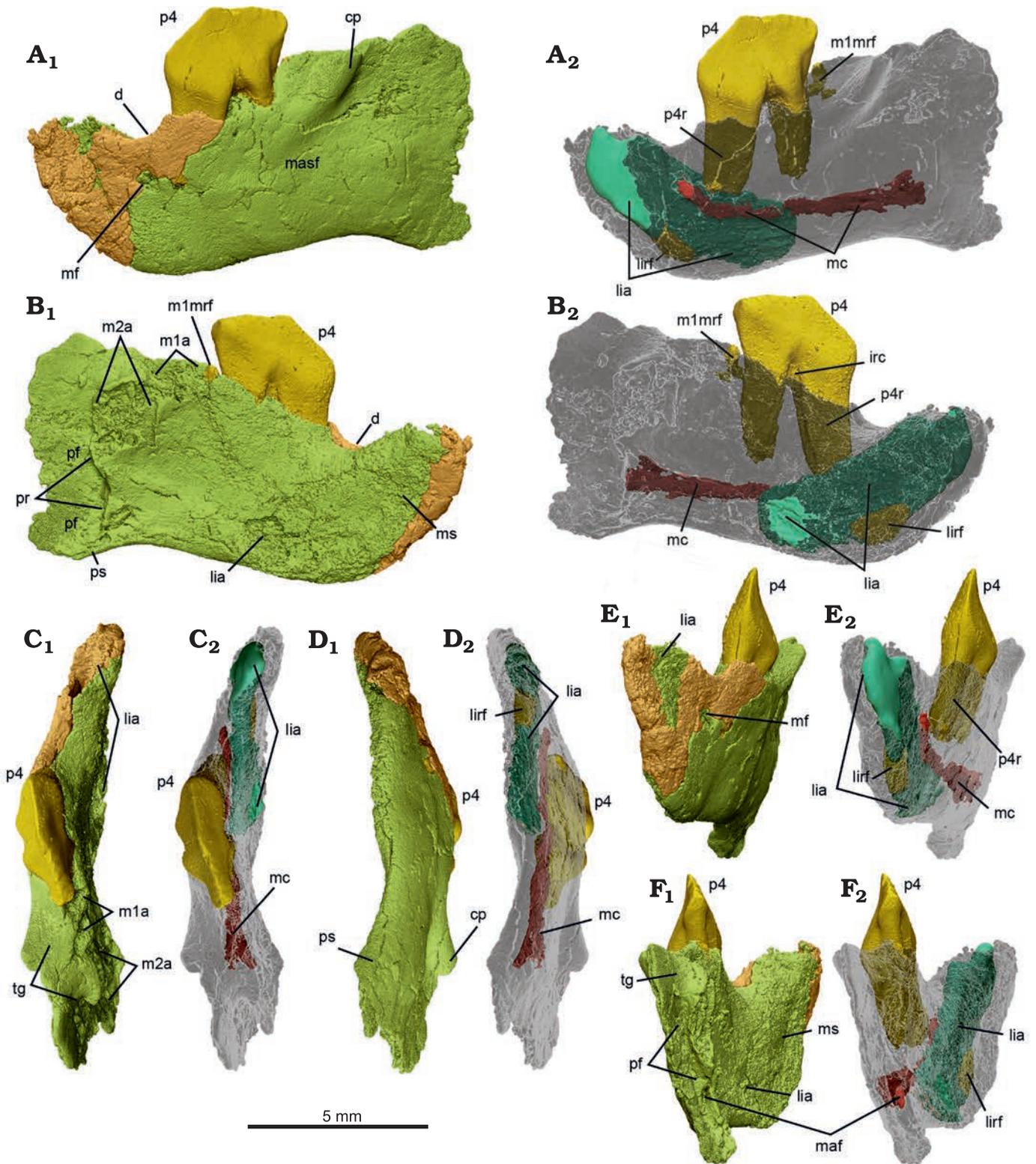


Fig. 4. MicroCT scans of left dentary with p4 in situ, NMV P252730, of the cimolodontan multituberculate *Corriebaatar marywaltersae* Rich, Vickers-Rich, Flannery, Kear, Cantrill, Komarow, Kool, Pickering, Trusler, Morton, van Klaveren, and Fitzgerald, 2009, Flat Rocks locality, Eumeralla Formation, Barremian, Lower Cretaceous of Victoria, Australia. The two parts (anterior fragment in brown, posterior fragment in lime green) that compose the specimen, in lateral (A), medial (B), dorsal (C), ventral (D), anterior (E), and posterior (F) views, with dentary semi-transparent in A₂-F₂. Abbreviations: cp, coronoid process; d, diastema; irc, interradicular crest; lia, lower incisor alveolus (turquoise); lirf, root fragment (dark yellow) in lower incisor alveolus; m1a, lower first molar alveoli; m1mrf, root fragment (dark yellow) in mesial alveolus of m1; m2a, lower second molar alveoli; maf, mandibular foramen; masf, masseteric fossa; mc, mandibular canal (deep red); mf, mental foramen; ms, mandibular symphysis; p4, lower fourth premolar (bright yellow); p4r, lower fourth premolar root (dark yellow); pr, pterygoid rim; pf, pterygoid fossa; ps, pterygoid shelf; tg, temporal groove.

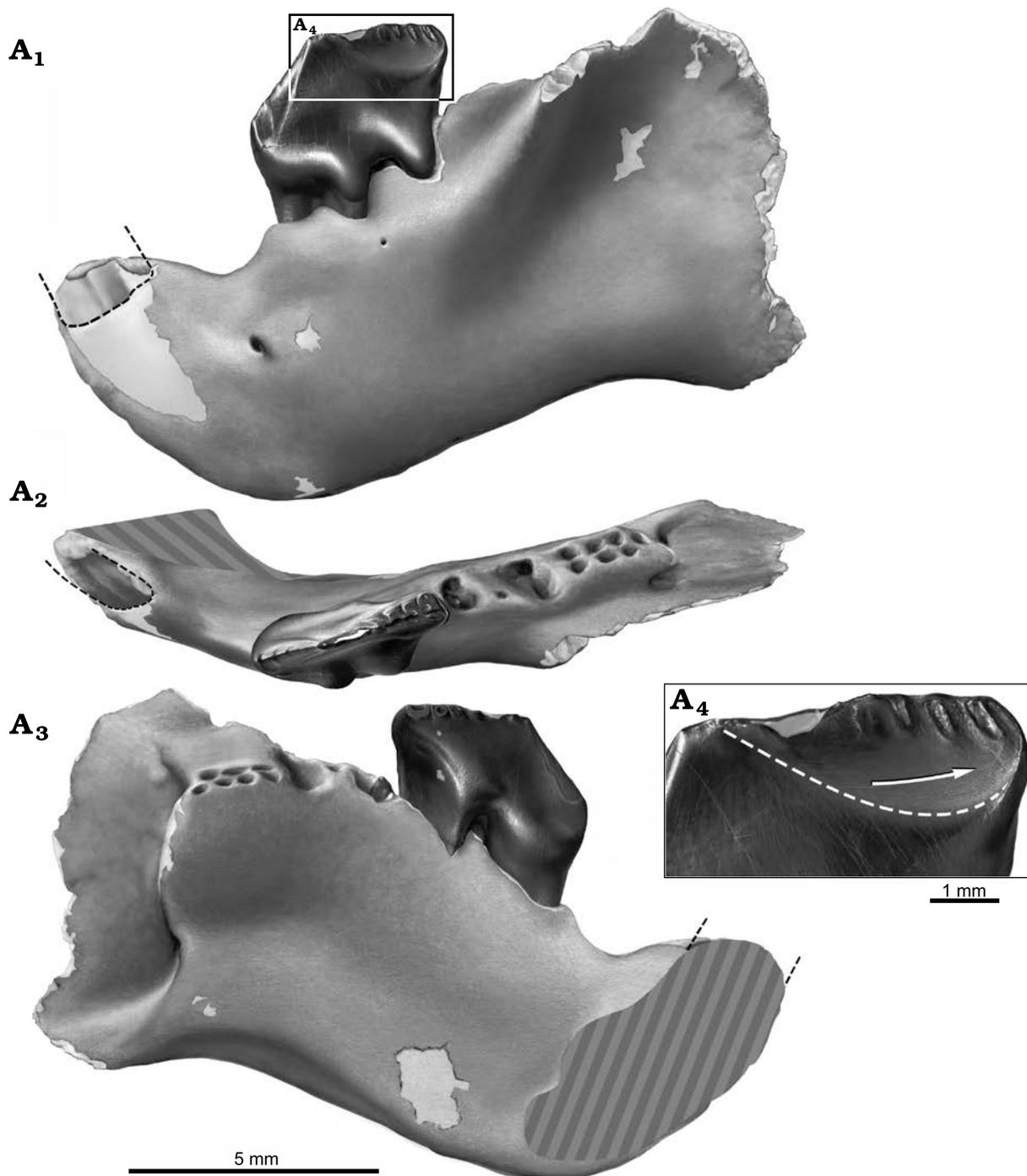


Fig. 5. Reconstruction of partial left dentary with p4 in situ, NMV P252730, of the cimolodontan multituberculate *Corriebaatar marywaltersae* Rich, Vickers-Rich, Flannery, Kear, Cantrill, Komarower, Kool, Pickering, Trusler, Morton, van Klaveren, and Fitzgerald, 2009, Flat Rocks locality, Eumeralla Formation, Barremian, Lower Cretaceous of Victoria, Australia. Specimen in lateral (A₁), dorsal/occlusal (A₂), and medial (A₃) views. Size and shape of base of crown of lower incisor indicated by black dashed lines. Estimate of size and position of symphyseal area indicated by gray hatching in A₂ and A₃. Buccal view of distal portion of p4 (A₄), illustrating abraded distobuccal wear facet, the lower limit of which is indicated by white dashed line. Buccal ridges are preserved as elliptical troughs of enamel surrounded by the abraded wear surface. Arrow indicates the slightly curved orientation of wear striations and the direction of palinal movement of p4 relative to the upper dentition. Artwork by Peter Trusler.

(the greatest buccolingual dimension) whereas the holotype p4 is 3.7 mm long and 1.6 mm wide. The length of the holotype is given as 3.4 mm in Rich et al. (2009) where it was evidently measured in a slightly different manner. On the mesial half of the crown, on the slope ascending to the first

serration, there are three faint “pseudoserrations” (sensu Krause 1982a) and associated short, faint buccal and lingual ridges, as on the holotype; the first pseudoserration is more prominent than the second, and the second is more prominent than the third. Whereas seven serrations are present

along the apical crest of the distal half of the p4 crown in the holotype, the number is more difficult to discern on NMV P216655 because of wear, although there is no evidence of a significant difference. Particularly striking is the presence of long narrow ridges descending ventromesially from the first serration, one on the buccal side and one on the lingual side of the crown, much better preserved on the less worn holotype. The lingual ridge is longer, extending to nearly the base of the crown. The ridges descending from the remaining serrations on both the buccal and lingual sides are extraordinarily short. Also much better preserved on the holotype is the distobuccal ledge. There is no trace of a buccal row of cusps (or cuspules) near the base of the crown (as is present in most plagiaulacidans). As on the holotype, there are two prominent but mesiodistally constricted exodaenodont lobes at the base of the crown on the buccal side, one on the mesial half and another on the distal half, with a strong dorsally directed concavity between them. There are two large roots supporting the crown, the larger mesial root being roughly triangular in cross section (approximating an isosceles triangle with the sharpest angle located mesially and a vertical groove located distally) and the smaller distal root being more rounded but also roughly triangular in cross section (but with the sharpest angle located distally and a vertical groove located mesially). A low interradicular crest spans the distance between the distal margin of the mesial root and the mesial margin of the distal root. The roots are approximately as long as the crown is tall and extend to roughly mid-height of the horizontal ramus.

Some wear features can be discerned on p4 of NMV P252730, but COVID restrictions precluded access to a scanning electron microscope that would have allowed adequate imaging of wear striations. Some wear appears to be present along the ascending mesial slope of the crown, the surface of which faces mesiobuccally. We assume that this was formed during the orthal slicing-crushing phase of mastication (Krause 1982b). A large, prominent, well-circumscribed wear facet is present on the buccal side of the distal slope, demarcated with a dashed white line in Fig. 5A₄. On this facet there are very slightly curved wear striations (visible using light microscopy) roughly parallel to the ventral margin of the dentary; the orientation of these striations and the direction of p4 movement relative to the upper cheek-teeth are also highlighted in Fig. 5A₄. If a comparison to jaw movement in species of the ptilodontoid multituberculate *Ptilodus* (Paleocene, North America) is valid, these striations were formed during the palinally-directed power stroke of the grinding cycle as p4 slid distally past the distolingual part of P4 (Krause 1982b).

The molars are not preserved in NMV P252730, except for a small fragment of a root in the mesial alveolus of m1. However, although the alveoli of the molar roots are not completely preserved and somewhat deformed, we were able to effectively visualize some basic aspects of their structure by using the microCT scans to digitally fill the alveolar voids to simulate the roots (Fig. 6).

Lying immediately distal to p4 are two large alveoli, one behind the other. We interpret these two alveoli to be for the primary mesial and distal roots of m1. The medial portions of the dorsal rims of both alveoli are broken away and not preserved, but that for the distal alveolus shows the most breakage. The shapes of these alveoli are not reliably discernible, but it appears that the mesial root was oval (the longest dimension oriented mesiolingually–distobuccally), whereas the distal root was larger and approximately in the shape of the numeral 8 in occlusal view (the longest dimension also oriented mesiolingually–distobuccally). Digitally infilling the alveoli (simulating mold-making compound) reveals that the two parts of this distal root diverged toward the root apices, with one part positioned mesiolingually and the other part distobuccally. As a rough estimate, judging from these two alveoli, m1 would have been about one-half the length of p4. In addition to the two primary alveoli, there is a much smaller alveolus, circular in cross section, for an accessory root (= intercalary root sensu Butler 1956) between the two primary alveoli and toward the buccal side.

Distal to the distal alveolus for m1 are several closely spaced, partial alveoli that we interpret to be for m2 based on the amount of space occupied. These alveoli lie slightly farther medially and ventrally than do the alveoli of m1 but there is some indication that deformation disrupted the alignment of m1 and m2. Relative sizes of any of the alveoli are difficult to reliably assess. The best-preserved alveolus for m2 is that for the mesiolingual root; this alveolus is bisected vertically, with the buccal half still fully intact and the lingual half broken away. Distal to the mesiolingual alveolus are at least two alveoli, aligned mesiodistally, with only their ventral, cup-shaped tips preserved. The ventral tips lie at approximately the same level as the ventral tip of the mesiolingual alveolus. There is probably an additional ventral tip in this row, indicative of a fourth alveolus preserved farther distally (indicated by dashed lines in Fig. 6A₁, A₂), but poor preservation precludes a definitive assessment. The void-filling exercise revealed the presence of an alveolus buccal to the mesiolingual alveolus, its full length likely not preserved. Distal to this mesiobuccal alveolus is one, perhaps two, additional alveoli but they are too poorly preserved to fully evaluate. Nonetheless, the parts of m2 alveoli preserved indicate that there were two rows of roots, one lying buccally and consisting of two or perhaps three roots and one lingually consisting of three or probably four roots. Despite the incompleteness of these alveoli, it is clear that those in the lingual row taper to the root terminus, thus indicating that the roots were “closed” and not ever-growing.

Another interpretation we considered was that there are two molars distal to m1. We do not, however, observe any change in size and orientation of the roots as there is between those of m1 and m2, and all of the roots distal to m1 are very closely spaced (Fig. 6). Furthermore, the bone supporting the toothrow appears to naturally end distal to this series of roots, which is roughly aligned with the posterior terminus of the temporal groove. We therefore regard the

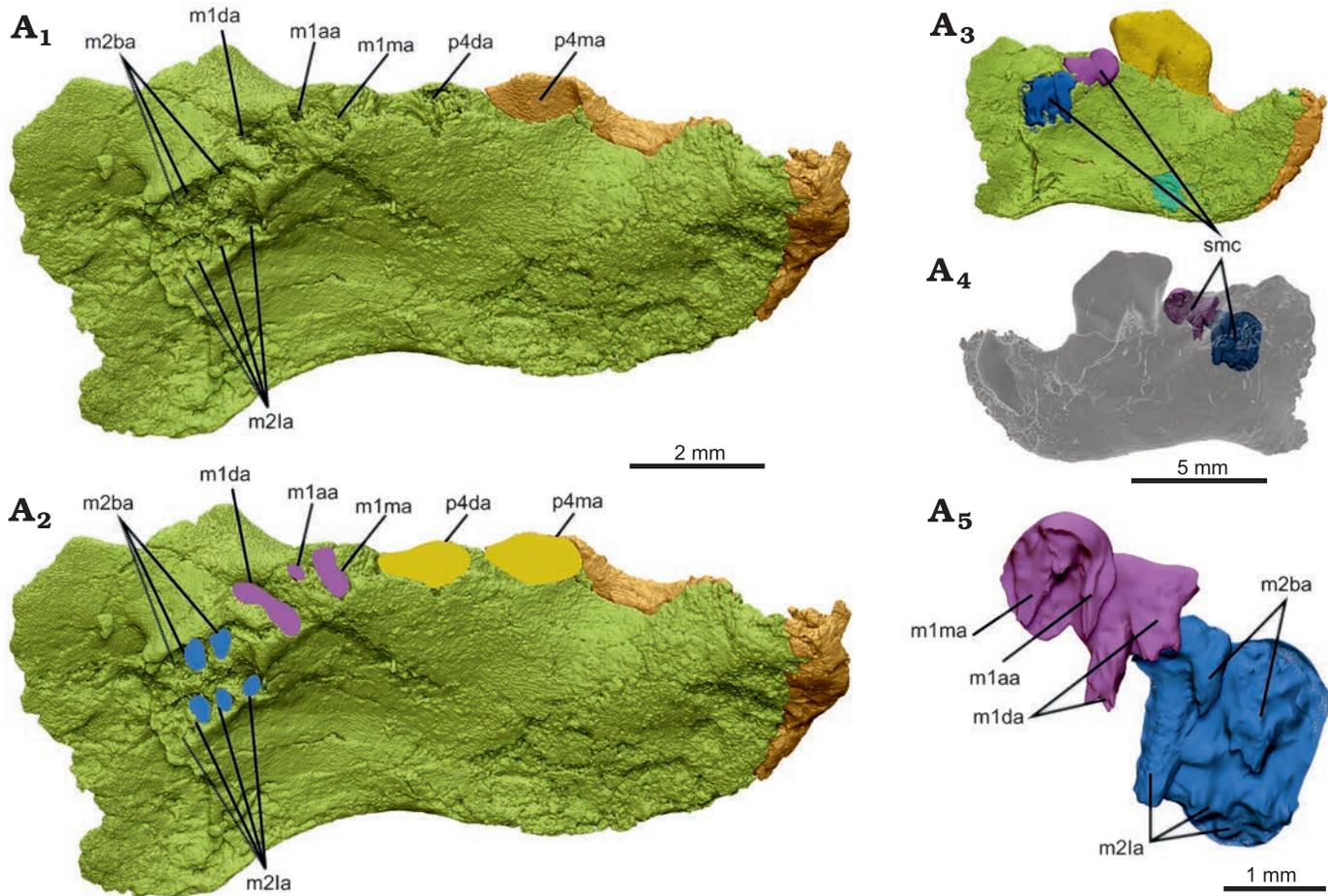


Fig 6. Interpretation of molar alveolar structure in dentary, NMV P252730, of the cimolodontan multituberculate *Corriebaatar marywaltersae* Rich, Vickers-Rich, Flannery, Kear, Cantrill, Komarow, Kool, Pickering, Trusler, Morton, van Klaveren, and Fitzgerald, 2009, Flat Rocks locality, Eumeralla Formation, Barremian, Lower Cretaceous of Victoria, Australia. Partial left dentary in dorsomedial view with p4 digitally extracted (A₁), outlines of interpreted alveoli for p4 (yellow), m1 (purple), and m2 (blue) (A₂). Medial (A₃) and lateral (A₄) views of dentary with computer-simulated mold-making compound overlying the partially preserved alveoli of m1 and m2 and filling the voids. A₃ and A₄ are views of entire specimen to provide context, dentary semi-transparent in A₄. Simulated mold-making compound enlarged (A₅) showing the parts that filled the voids of the partially preserved alveoli. Abbreviations: m1aa, m1 accessory alveolus; m1da, m1 distal alveolus; m1ma, m1 mesial alveolus; m2ba, m2 buccal alveoli; m2la, m2 lingual alveoli; p4da, p4 distal alveolus; p4ma, p4 mesial alveolus; smc, simulated mold-making compound. Note that m1da divides as it descends ventrally (contrast view in A₁, A₂ with that in A₅).

more parsimonious interpretation to be that there is only one molar behind m1 and that, tentatively, the lower dental formula is 1.0.1.2. Assuming that *C. marywaltersae* had only two molars and acknowledging that poor preservation precludes accurate measurement, we estimate the length of m1 to have been approximately 1.86 mm and the length of m2 to have been approximately 1.74 mm. It thus appears that m2 was approximately 94% the length of m1.

The dentary of NMV P252730 is rodentiform and includes virtually all of the horizontal ramus and anterior parts of the ascending process. As such, it does not preserve the posterior aspects of the masseteric fossa laterally or the pterygoid fossa medially, most of the coronoid process (dorsally and posteriorly), the pterygoid fovea, the condylar process, or the condyle. In lateral outline, in addition to the dorsally concave diastema described above, it is noteworthy that the ventral margin of the dentary is sinuous, being strongly convex anteroventrally (anteroventral to the lower incisor alve-

olus) and markedly concave beneath the molars (the apex of the concavity situated beneath m2), with the beginnings of a convexity that formed the ventral margin of the ascending process posteriorly. Although the strongly downturned aspect posteriorly gives the visual impression of a potential angular process more posteriorly, we conclude that an angular process was not present because: (i) the area posterior to the downturned area is clearly broken and the more posterior regions of the ascending ramus are not preserved; (ii) whereas most Mesozoic mammaliaforms exhibit a flat or convex ventral margin, such a strong concavity ventral to the cheek-teeth is known to occur in species of several other Mesozoic and Paleogene mammaliaform genera (e.g., *Galulatherium*, Krause et al. 2003; O'Connor et al. 2019; *Volaticotherium*, Meng et al. 2006), particularly multituberculates (e.g., *Allokosmodon*, Fox 2005; *Heishanobaatar*, Kusuhashi et al. 2010; *Meniscoessus*, Archibald 1982; *Microkosmodon*, Fox 2005; *Taeniolabis*, Granger and Simpson 1929; *Zofiabaatar*,

Carpenter 1998); and (iii) it would be unprecedented among Mammaliaformes to have an angular process positioned so far anteriorly on the dentary, at a dorsoventral level immediately posterior to the cheekteeth (Grossnickle et al. 2021).

The lateral side of the dentary exhibits a number of features (Fig. 4A). A single mental foramen is present just above mid-height of the horizontal ramus and below the nadir of the diastema. A much smaller foramen, most likely a nutrient foramen, is present posterior to the proximal part of the mesial root of p4. A masseteric foramen (see discussion of homologies in Krause et al. 2020b) in the anterior part of the masseteric fossa is absent. The anterior root of the coronoid process is represented by a prominent rounded ridge lateral to m1 that bulges laterally and extends anteroventrally–posterodorsally. A portion of this anterior root of the coronoid process is also observable on the holotype specimen, NMV P216655 (Rich et al. 2009: figs. 1A, 2B). The height and posterior extent of the coronoid process cannot be established on either specimen, because these areas are broken away. It is likewise not possible to reasonably estimate the angle between the anterior root and the alveolar plane of the molars, a character frequently used in phylogenetic analyses of mammaliaforms (e.g., Luo et al. 2015, 2017; Han et al. 2017; Krause et al. 2014, 2020a; Wang et al. 2021), because the coronoid process is so incomplete and the preserved alveoli are too deformed and broken.

As in other mammals, the anterior root of the coronoid process forms the anterodorsal border of the masseteric fossa. The masseteric fossa, as a whole, however, is not well delimited, in part because the anterodorsal border of the coronoid process becomes much less prominent as it descends anteroventrally. Nonetheless, it clearly extends anteriorly to below p4, perhaps as far as to the area below the mesial root. The masseteric crest (sensu Gambaryan and Kielan-Jaworowska 1995), defining the anteroventral border of the masseteric fossa, however, is represented only by a low, faint, rounded ridge; it is almost indiscernible, perhaps a result of deformation. Similarly, a masseteric fovea (sensu Gambaryan and Kielan-Jaworowska 1995) anterior to the masseteric fossa and a masseteric line (sensu Gambaryan and Kielan-Jaworowska 1995) extending posteriorly from the masseteric crest along the ventral border of the ascending ramus are not in evidence.

Medial to the anterior root of the coronoid process in the new specimen is a well-developed temporal groove (sulcus temporalis of Gambaryan and Kielan-Jaworowska 1995), best seen in dorsal view (Fig. 4C). It passes from lateral to m1 to almost as far posteriorly as the distal end of m2. At this point it terminates abruptly, because it intersects nearly perpendicular to the anterior end of the pterygoid fossa. The surface of the temporal groove is dorsally convex from anterior to posterior, whereas it is dorsally concave from lateral to medial. There is no trace in this region of a coronoid bone, rudimentary or otherwise.

On the medial side of the dentary (Fig. 4B) there is a large planar area (flat medially) anteriorly that represents

the mandibular symphysis, which was unfused. Although the relatively poor preservation of this side precludes precise delimitation of the margins of the symphysis, it appears to have extended posteriorly to at least the level of the posterior part of the diastema, and probably as far back as the mesial root of p4. Posterior to the symphysis, the medial side of the dentary is gently concave, but some aspects of this may be owing to mediolateral compression of the specimen. Immediately posterior to the distal alveoli of m2, the medial side of the dentary is interrupted by a strong crest that descends essentially vertically. This crest, termed the “pterygoid rim” here (because the term “pterygoid crest” has occasionally been used as a synonym for pterygoid shelf), is in precisely the position and orientation that one would expect for multituberculates and marks the anteromedial boundary of the pterygoid fossa, for insertion of the large medial pterygoid muscle that is so typical of multituberculates (Gambaryan and Kielan-Jaworowska 1995). The presence of a large pterygoid fossa is also clearly visible in posterior view (Fig. 4F), where mostly smooth (unbroken) bone is preserved, as a vertically elongate anterior concavity lateral to the pterygoid rim. Only a small part of the lateral wall of the pterygoid fossa is preserved, but it extends posteriorly well beyond the level of the pterygoid rim. The identity of the pterygoid fossa is further confirmed by the clear presence of a large oval (taller than wide) hole, the mandibular foramen (inferior dental foramen of Miao 1988).

A pterygoid shelf, forming the base of the pterygoid fossa, is not readily apparent although the anterior beginnings of it appear to be preserved because the ventral floor of the fossa is slightly wider than the area above it. Miao (1988) and Kielan-Jaworowska et al. (2004, 2005) have summarized different terms employed for the pterygoid shelf of multituberculates. We restrict the term here to the mediolaterally wide structure that forms the floor of the pterygoid fossa. By contrast, we restrict the term “pterygoid rim” to refer to the more-or-less vertical crest that descends ventrally from posterior to m2, intersecting the pterygoid shelf along the ventral margin of the dentary. In other words, the pterygoid rim forms the lateral edge of the anterior wall of the pterygoid fossa, even though the anterior–most aspect of the wall may be situated slightly farther anteriorly than the rim itself, creating a vertically aligned pocket.

There is no evidence of a postdentary trough or attachment of postdentary bones in *Corriebaatar marywaltersae*; absence of these features seems highly probable in NMV P252730 even without complete preservation of the most posterior aspects of the ascending ramus. A Meckelian sulcus and a dental lamina are also absent.

The microCT scans also reveal several features internally, in addition to the roots of p4 and the alveoli of the lower incisor and the molars described above (Fig. 4A₂–F₂). There is, for instance, a small fragment of the lower incisor root located deep within the alveolus anteroventrally. Correspondingly, there is a small root fragment preserved within the mesial alveolus of m1. Neither of these fragments

is large enough to yield any meaningful insights into the morphology of either of the roots or the crowns of these teeth. Also revealed on the scans is a small interradicular crest between the mesial and distal roots of p4. Most significantly, a canal, extending anteriorly and then antero-dorsally, passes from the mandibular foramen inside the pterygoid fossa to the mental foramen on the lateral side of the dentary, below the diastema. This is the mandibular canal, which is more or less complete and coherent save for a few vertical fractures and a few connections to other voids in the horizontal ramus. The canal served as passage for the inferior alveolar neurovascular bundle.

Discussion

The concept of the mammalian subclass Allotheria is not stable and has expanded from the two main groups (Haramiyida and Multituberculata) included in the most recent comprehensive compendium of Mesozoic mammaliomorphs by Kielan-Jaworowska et al. (2004) to also include two additional major clades, Gondwanatheria and Euharamiyida (see recent review in Hoffmann et al. 2020). Since Allotheria was first proposed by Marsh (1880), several other taxa (e.g., Tritylodontidae, Cope 1884; Kollikodontidae, Musser 2005; Musser et al. 2019) have also been suggested to belong to the group but are not currently included. In all phylogenetic analyses by Hoffmann et al. (2020) in which Allotheria was resolved as a clade, the enigmatic *Cifelliodon* was also included, but this taxon is not considered further here because it is not represented by lower jaw material or any lower teeth (Huttenlocker et al. 2018). In this context, we compare the known anatomy of *Corriebaatar* with that of haramiyidans, multituberculates, euharamiyidans, and gondwanatherians. For the purposes here, we do not include the enigmatic and highly controversial Ferugliotheriidae in Gondwanatheria and consider it separately.

Haramiyida.—Placement of Haramiyida outside of Mammaliaformes or within Allotheria is controversial, the history of which has been recently reviewed by Hoffmann et al. (2020), who recovered Haramiyida outside of Mammaliaformes in their parsimony and tip-dated Bayesian analyses but in a polytomy with other allotherians in their undated Bayesian analyses. Also controversial is the composition of Haramiyida but, pending resolution of these controversies, we include here a comparison of the lower jaw of *Corriebaatar marywaltersae* with that of the only two known unquestioned haramiyidans represented by lower jaw material, the Late Triassic *Haramiyavia clemmenseni* (see Jenkins et al. 1997; Luo et al. 2015) and *Kalaallitkigun jenkinsi* (see Sulej et al. 2020).

The lower jaws of *Corriebaatar* on the one hand and *Haramiyavia* and *Kalaallitkigun* on the other have little in common in that those of the latter exhibit a host of relatively plesiomorphic characteristics that are not present in

Corriebaatar. Collectively, these include a lower dental formula of 3.1.4.3 (and associated absence of a sizeable diastema), a long and shallow horizontal ramus, a prominent postdentary trough and Meckelian sulcus, presence of a coronoid bone (as indicated by a scar), a coronoid process that originates almost fully posterior to the cheektooth row and is not laterally separated from it by a wide temporal groove, a masseteric fossa that does not extend anteriorly onto the horizontal ramus, and absence of a pterygoid fossa and associated pterygoid shelf and rim. Furthermore, the mode of chewing in haramiyidans is inferred to have retained a significant orthal component rather than being strictly palinal (e.g., Butler 2000; Butler and Hooker 2005; Luo et al. 2015). A few attributes are shared with *Corriebaatar* (e.g., absence of dental lamina groove, unfused mandibular symphysis, absence of masseteric foramen) but these are features that are either lost near the stem of the mammaliomorph phylogenetic tree or are highly variable in their occurrence across the tree (e.g., Hoffmann et al. 2020). It should also be noted that *Haramiyavia clemmenseni*, in the only known specimen, has one (left) or two (right) mental foramina placed at mid-height or below mid-height on the horizontal ramus whereas *C. marywaltersae*, in the only specimen in which the condition can be documented, has only one placed above mid-height. This area is not preserved in the dentary of *Kalaallitkigun jenkinsi*.

The dentition of *C. marywaltersae* differs markedly from that of haramiyidans. In addition to the fact that there are far fewer teeth in *C. marywaltersae* (lower dental formula 1.0.1.2 vs. 3.1.4.3), the lower central incisor is relatively much enlarged and more laterally compressed, and p4 is fully plagiaulacoid (i.e., laterally compressed and blade-like), which is not the case in *H. clemmenseni* and other haramiyidans (Jenkins et al. 1997; Hahn and Hahn 2006; Luo et al. 2015). These teeth are not preserved in the specimen of *K. jenkinsi*. In sum, the overwhelming balance of morphological differences makes it extremely unlikely that *Corriebaatar* is a haramiyidan.

Multituberculata.—Multituberculata is the core group of Allotheria, phylogenetically defined by Sereno (2006) as the most inclusive clade including *Taeniolabis taoensis* but not *Mus musculus* and *Ornithorhynchus anatinus*, and has been since Marsh (1880) erected the subclass over 140 years ago. Multituberculates are arguably the most successful of early mammaliaforms, with a temporal range extending from the Middle Jurassic to the late Eocene (Kielan-Jaworowska et al. 2004; Butler and Hooker 2005; Schumaker and Kihm 2006; Dawson and Constenius 2018) and were also among the most speciose and diverse mammals in the northern supercontinent Laurasia, particularly North America, in the Late Cretaceous and early Paleogene (Krause 1986; Cifelli et al. 2004; Kielan-Jaworowska et al. 2004; Weil and Krause 2008). Documentation of their presence in Gondwana, by contrast, has been challenging and controversial.

Unfortunately, the posterior end of the ascending ramus in NMV P252730 is not preserved and cannot be evaluated

for phylogenetic character states. However, in comparison to other mammaliaforms, the suite of morphological features exhibited by the new dentary of *Corriebaatar marywaltersae* is consistent with placement in Multituberculata, as originally concluded by Rich et al. (2009) on the basis of p4 morphology alone. These features include: (i) absence of the postdentary trough and attached postdentary bones; (ii) absence of the Meckelian sulcus; (iii) absence of a groove for dental lamina; (iv) absence of a coronoid bone (the paulchoffatiid *Kuehneodon* is the only multituberculate known to retain a remnant of this element, Hahn 1977); (v) a large pterygoid fossa with an associated strong pterygoid rim (defined in the “Description” section; see Fig. 4B₁) and presence of a pterygoid shelf (tentatively identified in NMV P252730 based on its anterior beginning); (vi) position of the mandibular foramen inside the pterygoid fossa and below the alveolar plane; (vii) a distinct anterior root of the coronoid process beginning far anteriorly (lateral to the molars and separated from them by a distinct temporal groove) and forming the anterodorsal border of the masseteric fossa; (viii) anterior extension of the masseteric fossa onto the horizontal ramus up to level of at least m1; (ix) absence of a masseteric foramen; (x) presence of a distinct diastema between the lower incisor and the first cheektooth; (xi) presence of a single mental foramen, situated ventral to the diastema; (xii) horizontal ramus short and deep; and (xiii) longitudinal axis of the incisor crown and its root positioned oblique to the longitudinal axis of the cheektooth row, resulting in a marked external angle between anterior and posterior parts of the horizontal ramus in dorsal (or ventral) view (the paulchoffatiid *Paulchoffatia* is unique among multituberculates in not exhibiting such an obliquity between the longitudinal axes of the incisor and the postcanine tooth row, Hahn 1971). With the stated exceptions, these features are almost ubiquitously present in multituberculates, including early-branching forms such as the paulchoffatiids *Rugosodon* (Yuan et al. 2013), *Paulchoffatia* (Hahn 1969), and *Kuehneodon* (Hahn 1969); the plagiaulacid *Plagiaulax* (Simpson 1928, Ride 1957); and the eobaatarids *Sinobaatar* (Kusuhashi et al. 2009) and *Jeholbaatar* (Wang et al. 2019). The exceptions (coronoid bone in *Kuehneodon*, lack of oblique angle between anterior and posterior parts of horizontal ramus in *Paulchoffatia*) support a higher position on the multituberculate phylogenetic tree for *Corriebaatar* than these early-branching paulchoffatiids.

Two features of the dentary stated to be characteristic of multituberculates (Gambaryan and Kielan-Jaworowska 1995) are not strongly developed in *Corriebaatar*: (i) a distinct masseteric crest forming the anteroventral border of the masseteric fossa (and continuing posteriorly as a masseteric line along the ventral margin of the ascending process), and (ii) a masseteric fovea, anterior to the masseteric crest, and, according to Gambaryan and Kielan-Jaworowska (1995), serving as the insertion area for the masseter medialis pars anterior. A broader survey of multituberculates, however, reveals that these two features are variably developed in this group. A masseteric

crest is only faintly visible in NMV P252730, presenting as a low, rounded ridge, but such is also the case in several other multituberculates (e.g., *Cimexomys minor*, Sloan and Van Valen 1965: fig. 2G; *Nessovbaatar multicostatus*, Kielan-Jaworowska and Hurum 1997). A masseteric fovea is strongly delimited in a few genera like *Chulsanbaatar*, *Catopsbaatar*, *Guibaatar*, *Guimarotodon*, *Meketibolodon*, and *Stygimys*, but it is not ubiquitous in multituberculates and, indeed, is poorly developed “in most genera” and confluent with the masseteric fossa (Gambaryan and Kielan-Jaworowska 1995: 54; Hahn and Hahn 1998; Kielan-Jaworowska et al. 2004, 2005; Wible et al. 2019). We tentatively consider the poor development of these features to not preclude assignment of *Corriebaatar* to Multituberculata.

The dentition of *Corriebaatar* remains poorly known, limited to p4 and what can be gleaned from the alveoli for the lower incisor and lower molars. However, all that is known of the dentition is also consistent with placement in Multituberculata and, more specifically, in Cimolodonta. The presence of a single lower incisor separated from p3 or p4 by a distinct diastema is ubiquitous across Cimolodonta. The fact that the lower incisor of *Corriebaatar* is large, robust, and significantly compressed mediolaterally (and likely ever-growing) is a derived feature (more derived than in all “plagiaulacidans”, with the possible exception of *Glirodont*; Engelmann and Callison 1999) and is characteristic of a host of cimolodontan multituberculates, including djadochtatherioids, taeniolabidoids, microcosmodontids, and eucosmodontids. Furthermore, the erect angle of the incisor is not unlike that of *Lambdopsalis*, *Taeniolabis*, and various djadochtatherioids such as *Sloanbaatar*, *Kryptobaatar*, *Djadochtatherium*, *Catopsbaatar*, and *Mangasbaatar* (Rougier et al. 2016: fig. 31).

The absence of p3 (as well as p1 and p2) is an apomorphic trait and is also indicative of cimolodontan affinities: p3 is present in all “plagiaulacidans” for which the condition is known and in most but certainly not all cimolodontans; p3 is absent in all taeniolabidids and lambdopsalids, in some and perhaps all kogaionids (see Smith et al. 2021), and in some neoplagiaulacids, eucosmodontids, and microcosmodontids (Krause et al. 2020c: table 4).

Aside from a couple of features that can be considered autapomorphies for *Corriebaatar*, and therefore diagnostic of the taxon, its p4 is typical of that in multituberculates in being laterally compressed and blade-like, with a row of serrations and associated buccal and lingual ridges, and anchored by two long, stout roots, the mesial one being more robust than the distal one, a condition regarded as typical for cimolodontans but not plagiaulacidans (Kielan-Jaworowska et al. 2007). The roots are also connected by a low interradicular crest, which is frequently encountered in cimolodontan p4s (e.g., *Anconodon*, *Cimexomys*, *Cimolomys*, *Ectypodus*, *Meniscoessus*, *Mesodma*, *Neoplagiaulax*, *Ptilodus*, *Tashtykia*, and *Uzbekbaatar*, Sahni 1972; Kielan-Jaworowska and Nesson 1992; Eberle and Lillegraven 1998; Scott 2005; Scott and Krause 2006, Averianov et al. 2021). The

shape of p4 of *Corriebaatar* is unusual for a multituberculate in that it exhibits a peaked apex on the crown at approximately mid-length (rather than more mesially), but this is not unprecedented among multituberculates, both basal (*Kermackodon*, Butler and Hooker 2005) and derived (e.g., *Fractinus*, Higgins 2003; *Xanclomys*, Rigby 1980; Lofgren et al. 2017). *Corriebaatar* lacks a basal row of cusps (or cuspules) buccally, which is present in most plagiaulacidans (Kielan-Jaworowska and Hurum 2001; Hahn and Hahn 2004, Averianov et al. 2021). The buccal and lingual ridges descending from the serrations along the apical crest of p4 of *Corriebaatar* are unusually short (all except those descending from the first serration), in contrast to the much longer ones present in most cimolodontans, but several other cimolodontan taxa also exhibit short ridges (e.g., *Barbatodon*, *Microcosmodon*, and *Yubaatar*, Csiki et al. 2005; Fox 2005; Xu et al. 2015; Smith et al. 2021), and ridges are entirely absent or rudimentary in cimolodontans with much-reduced p4s (e.g., *Catopsalis*, *Lambdopsalis*, *Prionessus*, *Shenopsalis*, *Taeniolabis*, and *Valenopsalis*, Granger and Simpson 1929; Sloan and Van Valen 1965; Miao 1986; Meng et al. 1998; Williamson et al. 2016). The short p4 ridges of *Corriebaatar* are also quite similar to those on some “plagiaulacidans” (see examples in Hahn and Hahn 2004: fig. 13a–d, f, g, l). Finally, the position of the wear facets on p4 and the wear striations within them are consistent with the palinal direction of jaw movement inferred for multituberculates (e.g., Krause 1982b, Gambaryan and Kielan-Jaworowska 1995).

The molars are not preserved in NMV P252730, but the alveoli for them demonstrate three aspects that are also consistent with inclusion of *Corriebaatar* in Multituberculata and further suggestive of cimolodontan affinities. First, m1 and m2 are each supported by more than just two roots. Accessory roots supporting the molars are not uncommon in multituberculates and have been documented for several cimolodontan genera (e.g., *Acheronodon*, *Allocosmodon*, *Catopsalis*, *Cimolodon*, *Cimolomys*, *Essonodon*, *Filikomys*, *Meniscoessus*, *Microcosmodon*, *Paessonodon*, *Pentacosmodon*, and *Taeniolabis*, Clemens 1964; Holtzman and Wolberg 1977; Krause 1977; Archibald 1982; Middleton 1982; Simmons 1987; Hunter et al. 1997; Fox 2005; Wilson et al. 2010; Scott et al. 2018; Weaver et al. 2020). Although the molar roots of “plagiaulacidans” appear to be less well known (or documented), Butler (2000: 336) stated that “the possession of three roots ... has not been observed in Jurassic multituberculates”. Consistent with that generalization, Hahn (1969, 1971) indicated that paulchoffatiids do not have accessory roots but, instead, two main roots that often coalesce (Hahn 1969, 1971). Similarly, Simpson (1928) made note of a plagiaulacid molar with only two roots. Finally, accessory molar roots were not noted by Hahn and Hahn (2004) in their review of “plagiaulacidan” dentitions or in descriptions of recently described, early branching forms like *Rugosodon* (Yuan et al. 2013) and *Jeholbaatar* (Wang et al. 2019). We have found reports of only two exceptions of more than two roots in “plagiaulacidan” molars but it must be noted

that these both pertain to upper, not lower, molars: (i) three probable roots (“due to division of the mesial root”) in an M2 of the hahnotheriid *Hahnotherium* (Butler and Hooker 2005: 199); and (ii) an M1 of the pinheirodontid *Teutonodon* bears a small accessory root between the two primary roots (Martin et al. 2016). Second, although the length of m1 can only be roughly estimated in NMV P252730 based on its preserved alveoli, it appears to have been only about one-half (~0.51 times) the length of p4; this ratio is present only in some of the more “specialized” multituberculates (e.g., *Arginbaatar*, *Anconodon*, *Eucosmodon*, *Prochetodon*, and *Ptilodus*) that have a relatively large p4 (Eaton and Cifelli 2001: table 2; Weil and Krause 2008). Third, the preserved molar alveoli in NMV P252730 of *Corriebaatar* indicate that m2 was slightly shorter than m1 (~0.94 times). With only a few exceptions (e.g., some members of the “*Paracimexomys* group” and the highly derived *Sphenopsalis*), m2 is shorter than m1 in cimolodontan multituberculates whereas m2 is approximately equal in length or longer than m1 in “plagiaulacidans” (Krause et al. 1992: table 2; Eaton and Cifelli 2001: table 2; Mao et al. 2016: table 2).

We conclude that the preserved morphology of the two known specimens of *C. marywaltersae* is consistent with assignment to Multituberculata and, more specifically, to Cimolodonta.

Non-ferugliotheriid Gondwanatheria.—Based on current evidence, Gondwanatheria is a strictly Late Cretaceous–early Paleogene Gondwanan clade. Although higher-order relationships of allotherians are beyond the scope of this study, it must be noted that the position of Gondwanatheria within Allotheria is far from established; in the recent phylogenetic analyses of Mammaliaformes by Hoffmann et al. (2020: 213), gondwanatherians were resolved “either as sister to Multituberculata, nested within Multituberculata, or as sister to *Cifelliodon* (and Euharamiyida), or in a polytomy with other allotherians.” Furthermore, as stated above, the Ferugliotheriidae (including *Ferugliotherium*, *Trapalcotherium*, and, tentatively, *Magallanodon*) are considered separately below. Although variations in placement occur, the non-ferugliotheriid gondwanatherians are currently thought to include the adalatheriid *Adalatherium*, the enigmatic *Galulatherium* (not firmly established as a gondwanatherian), and the sudamericids *Sudamerica*, *Gondwanatherium*, *Vintana*, *Greniodon*, *Bharattherium*, and *Lavanify*, with the last two genera being more closely related to one another than to any other gondwanatherian (Hoffmann et al. 2020).

The lower jaw of non-ferugliotheriid gondwanatherians is known from virtually complete dentaries of *Adalatherium hui* (see Krause et al. 2020a, b) and partial dentaries of *Sudamerica ameghinoi* (see Pascual et al. 1999), cf. *Sudamerica ameghinoi* (see Goin et al. 2006), *Gondwanatherium patagonicum* (see Bonaparte 1990; Gurovich 2001, 2006), and *Galulatherium jenkinsi* (see Krause et al. 2003; O’Connor et al. 2019). The specimens of cf. *Sudamerica ameghinoi* and *Gondwanatherium pata-*

gonicum are too fragmentary to be particularly informative in the current context, and identification of the latter as pertaining to *Gondwanatherium* has been questioned (Pascual et al. 1999; Rougier et al. 2021). Our comparisons of the lower jaw morphology of *Corriebaatar marywaltersae* are, therefore, restricted to the dentaries of *Adalatherium hui* (UA 9030), *Sudamerica ameghinoi* (MPEFCH 534), and *Galulatherium jenkinsi* (RRBP 02067).

It is important to underscore that the dentary characteristics listed above as being consistent with referral of *Corriebaatar* to Multituberculata do not all ineluctably exclude the possibility of referral to other allotherian taxa, including Gondwanatheria; indeed, many of these features may be plesiomorphic for Allotheria, or at least for a clade that unites multituberculates, gondwanatherians, and euharamiyidans. As such, the dentary specimens of *Adalatherium*, *Sudamerica*, and *Galulatherium*, collectively, exhibit almost all of the same dentary features listed above as being shared between *Corriebaatar* and multituberculates. There are two exceptions: (i) the anterior root of the coronoid process does not extend as far anteriorly relative to the cheekteeth as in *Corriebaatar* and, (ii) related to the previous condition, the masseteric fossa does not extend as far anteriorly on the horizontal ramus. Another difference is that the diastema is quite asymmetrical (more L-shaped) in the gondwanatherians *Adalatherium* and *Sudamerica* (but not *Galulatherium*) compared to that in *Corriebaatar* (more U-shaped), although it must be noted that some derived multituberculates also exhibit marked asymmetry in this regard (e.g., *Catopsbaatar* and *Taeniolabis*).

Whereas the morphology of the dentary of *Corriebaatar* is consistent with assignment to Multituberculata and/or Gondwanatheria, the lower dentition does not support gondwanatherian affinities. The morphology of p4, which is large, laterally compressed, and blade-like in *Corriebaatar*, is as in multituberculates but unlike any tooth in the lower dentition of non-ferugliotheriid gondwanatherians (also see discussion of Ferugliotheriidae below). The alveoli preserved in NMV P252730 are inferred to reveal the presence of two molariform cheekteeth distal to p4. Most gondwanatherians, by contrast, exhibit four molariform cheekteeth (Pascual et al. 1999; Krause et al. 2014, 2020c), although their homologies are debated (e.g., Pascual et al. 1999; Pascual and Ortiz-Jaureguizar 2007; Gurovich and Beck 2009). *Galulatherium* is the known exception in that it possesses four, columnar, enamel-less, ever-growing cheekteeth (O'Connor et al. 2019). Nonetheless, no non-ferugliotheriid gondwanatherian bears a plagiaulacoid cheektooth. Finally, the roots of the cheekteeth were not ever-growing in *Corriebaatar* like those in most non-ferugliotheriid gondwanatherians (those of *Adalatherium* and *Vintana* providing exceptions in this regard).

Euharamiyida.—Euharamiyidans are a clade of allotherian mammals with disputed members and taxonomic names (variously also referred to as Eleutherodonta, Eleutherodontida, and Eleutherodontidae) that were represented by isolated

teeth and are now known from additional relatively complete material, including lower jaws, from the Middle–Late Jurassic of China. Undoubted euharamiyidans represented by lower jaw material include *Arboroharamiya* (Zheng et al. 2013; Meng et al. 2014, 2018; Han et al. 2017), *Shenshou* (Bi et al. 2014), *Xianshou* (Bi et al. 2014), *Vilevolodon* (Luo et al. 2017; Wang et al. 2021), and *Qishou* (Mao and Meng 2019a). *Megaconus*, from the Middle Jurassic of China (Zhou et al. 2013), is a problematic taxon and is not considered here because of lingering controversies concerning its morphology (e.g., Bi et al. 2014; Meng et al. 2014; Han et al. 2017; Wang et al. 2021) and because it is unstable in recent phylogenies (e.g., Bi et al. 2014; Luo et al. 2017; Huttenlocker et al. 2018; Hoffman et al. 2020; Wang et al. 2021).

Like multituberculates and/or gondwanatherians, the lower jaws of euharamiyidans share a number of features with that of *Corriebaatar*. These include: dentary short and deep; lower dental formula 1.0.1.2; absence of postdentary trough, postdentary bones, and Meckelian sulcus (for clarification, see Wang et al. 2021); presence of diastema between lower incisor and cheekteeth; absence of groove for dental lamina; presence of prominent pterygoid fossa with associated pterygoid shelf and rim; masseteric fossa extending far anteriorly on horizontal ramus; a mandibular foramen situated in pterygoid fossa, below alveolar plane; absence of masseteric foramen; and unfused mandibular symphysis. The lower jaws of euharamiyidans are plesiomorphic relative to those of *Corriebaatar* in a few features: presence of vestigial coronoid bone (but apparently absent in *Vilevolodon*, Wang et al. 2021), long axis of incisor aligned with cheektooth row (see Mao and Meng 2019a: fig. 2), and retention of at least some orthal component in the movement of the lower jaw during chewing (Luo et al. 2017; Mao and Meng 2019b). They are also specialized in their own right in possessing a dentary that is extraordinarily thin (mediolaterally) and gracile and in having an angular process that may or may not be homologous with that of other mammaliaforms. Somewhat controversial is the position of the mental foramen in euharamiyidans, scored as “in the canine and anterior premolar (premolariform) region” in *Arboroharamiya*, *Shenshou*, *Xianshou*, and *Vilevolodon* by Luo et al. (2015, 2017), “at the ultimate premolar and the first molar junction” by Han et al. (2017: 37, supplementary information), and illustrated as below the diastema (between the lower incisor and p4) in *Vilevolodon* by Wang et al. (2021: extended data fig. 3a, d) and in *Qishou*, which has two foramina, by Mao and Meng (2019a: fig. 2). Overall, lower jaws of genera traditionally included in Euharamiyida and of *Corriebaatar* are similar in some respects, but those of the former are more plesiomorphic in some aspects of their morphology and more specialized in others.

The dentitions of Euharamiyida and *Corriebaatar* are quite different. The lower incisor in euharamiyidans is large and has a long root but is not strongly compressed mediolaterally nor robust like that of *Corriebaatar*. Furthermore, the lower incisor root in euharamiyidans is tapered, indicating

finite growth, which is likely not the case for *Corriebaatar*. The tooth identified as a p4 in euharamiyidans is, like that of *Corriebaatar*, supported by two stout roots and has a crown that is tall, laterally compressed, and considerably longer than m1. There are two important differences, however, in that the p4 crown in euharamiyidans rises to a single, tall mesial cusp followed distally by a basin or basin-like structure bearing several minor cusps on its rim. By contrast, the crown of *Corriebaatar* is arched, has multiple serrations (coupled with short buccal and lingual ridges), and no basin. Finally, the lower molars of euharamiyidans appear to have multiple roots, which is also the condition in *Corriebaatar*, but they are all fused proximally and were housed in a single large alveolus (Bi et al. 2014; Meng et al. 2014; Luo et al. 2017), thus differing dramatically from the multiple, small, separate alveoli for fully divided roots supporting m1 and m2 in *Corriebaatar*.

Ferugliotheriidae.—*Ferugliotherium windhauseni* from the latest Cretaceous (Maastrichtian) of Argentina includes two junior synonyms, *Vucetichia gracilis* (see Krause 1993) and *Argentodites coloniensis* (see Gurovich and Beck 2009; Brown et al. 2020; Rougier et al. 2021). Whether or not the similarly sized *Trapalcotherium matuastensis*, known only from a single incomplete m1 from the Allen Formation (Rougier et al. 2009), is a distinct genus and species is debatable and awaits the recovery of more complete material. Also debatable is whether or not the relatively large but low-crowned *Magallanodon baikashkenke*, known from several molariform teeth, an upper incisor, and a small fragment of dentary, should be included in Ferugliotheriidae (Goin et al. 2020; Chimento et al. 2020, 2021; Rougier et al. 2021). It is noteworthy that the molariform teeth of *Magallanodon*, like those of *Ferugliotherium* and *Corriebaatar*, have more than two roots (the number of roots on the molariform of *Trapalcotherium* is unknown). The dentary fragment of *Magallanodon*, consisting of an anterior portion of the horizontal ramus, demonstrates the presence of an unfused mandibular symphysis, a large, laterally compressed, long-rooted incisor, a dorsally concave diastema, a single, dorsally placed mental foramen, and a masseteric fossa that extends far anteriorly (Chimento et al. 2021). Although the molariform teeth are distinctive, these features of the dentary do not meaningfully differentiate *Magallanodon* from those of gondwanatherians, multituberculates, euharamiyidans, or *Corriebaatar*; *Magallanodon* is therefore not considered further here.

The affinities of *Ferugliotherium*, whether a multituberculate or an early branching gondwanatherian, are controversial (see review in Rougier et al. 2021). A recent analysis by Hoffmann et al. (2020) found conflicting support: parsimony analyses recovered ferugliotheriids within Gondwanatheria (and outside of Multituberculata), tip-dated Bayesian analyses nested ferugliotheriids within Multituberculata (and outside of Gondwanatheria), and undated Bayesian analyses found Gondwanatheria (including *Ferugliotherium* and *Trapalcotherium*) within Multituberculata. Brown et

al. (2020), however, on the basis of new gnathic and dental material from the La Colonia Formation (not included in the analysis by Hoffmann et al. 2020) were able to formally synonymize *Argentodites* with *Ferugliotherium* and argued persuasively for multituberculate affinities. Correspondingly, Rougier et al. (2021: 303) argued that the morphology of the dentary and the presence of a large incisor, a sizeable diastema, a plagiulacoid premolar, and two molariforms in *Ferugliotherium*, “is congruent with that of cimolodont multituberculates.” We eagerly await the description of the new material but, for our purposes here, provisionally accept the conclusion that *Ferugliotherium* is a cimolodontan multituberculate. However, we also acknowledge the conundrum presented by the pattern of cusps on the molariforms; it is similar to that of more hypsodont gondwanatherians, as first established by Krause and Bonaparte (1993) and recently reemphasized by Goin et al. (2020).

With the exception of the as-yet-undescribed dentaries containing p4 announced by Brown et al. (2020), knowledge of the lower jaw morphology of ferugliotheriids is restricted to the single small dentary fragment (MACN-RN 975) tentatively referred to *Ferugliotherium windhauseni* by Kielan-Jaworowska and Bonaparte (1996). Accepting the conclusion that the ferugliotheriid molariforms are associated with the plagiulacoid premolars (Brown et al. 2020; Rougier et al. 2021), *Ferugliotherium* exhibits the following features that are shared with *Corriebaatar*: small size (p4 length 4.15–4.8 mm, Kielan-Jaworowska and Bonaparte 1996; Kielan-Jaworowska et al. 2007); lower dental formula of 1.0.1.2 (and therefore absence of p3); large, laterally compressed lower incisor, the root of which extends posteriorly to the level of p4; short diastema (shorter than the length of p4); plagiulacoid p4 with arcuate dorsal outline (contra Kielan-Jaworowska et al. 2007; see Gurovich and Beck 2009), low number of serrations (7 in *Corriebaatar*, 8 in *Ferugliotherium*), and mesial root more robust than distal root; two lower molariform teeth with multiple, non-hypsodont roots; single mental foramen situated above mid-height on horizontal ramus; distinct angle between anterior and posterior parts of the horizontal ramus; and palinal stroke of grinding cycle (Krause et al. 1992; Krause and Bonaparte 1993; Kielan-Jaworowska and Bonaparte 1996; Kielan-Jaworowska et al. 2007; Brown et al. 2020). Despite these similarities, they are quite different in details, primarily in that the ridges descending from the serrations of p4 in *Ferugliotherium* are long (more typical of cimolodontans in general) and those of *Corriebaatar*, except those descending from the first serration, are extraordinarily short. In this context, the short ridges of *Corriebaatar* are considered to be autapomorphic. It is, however, worth observing that p4 of *Ferugliotherium* appears to have at least incipiently developed the double exodaenodont lobes (Kielan-Jaworowska et al. 2007) that are so characteristic of *Corriebaatar*. The implications of this observation can only be evaluated with more complete remains of both *C. marywaltersae* and *F. windhauseni* (or new, closely related taxa) but current ev-

idence leads us to formulate the working hypothesis that these two taxa may belong to the same lineage of cimolodontan multituberculates.

Concluding remarks

Phylogenetic placement.—Although the character states of *Corriebaatar marywaltersae* revealed by the dentary in NMV P252730 and p4 in both NMV P216655 (the holotype) and NMV P252730 support the conclusion that it is a cimolodontan multituberculate, we eagerly look forward to recovering more material that would allow us to more meaningfully incorporate the genus into a phylogenetic analysis and thus more precisely understand its relationships within Cimolodonta. Indeed, cimolodontan interrelationships are, in general, poorly understood (e.g., Cifelli 2001; Martin 2018) and, although most workers (e.g., Simmons 1993; Kielan-Jaworowska and Hurum 2001; Kielan-Jaworowska et al. 2004) regard the group as monophyletic, even this has been questioned (Hahn and Hahn 1999; Fox 2005). We summarize here our interpretations of phylogenetic placement of *Corriebaatar marywaltersae* within Allotheria based on the limited information available from the holotype and referred specimens.

The lower jaw morphology exhibited by the new specimen described in this report, NMV P252730, reveals a plethora of characters that are seen in multituberculates, gondwanatherians, and euharamiyidans and are much more derived than those of haramiyidans. Whereas features of the dentary are entirely consistent with assignment to Cimolodonta, the dentary of *Corriebaatar* differs from those of non-ferugliotheriid gondwanatherians in possessing a coronoid process that originates relatively far anteriorly and, correspondingly, a masseteric fossa that extends far anteriorly onto the horizontal ramus beyond the level of the molars. Similarly, the lower jaw of *Corriebaatar* differs from those of euharamiyidans in being generally much more robust, in that the long axis of the incisor is not aligned with the long axis of the cheektooth row, in lacking any trace of a Meckelian sulcus, and in having a fully palinal power stroke of the grinding cycle.

The dentition of *Corriebaatar*, consisting of a large, mediolaterally compressed lower incisor separated from a blade-like p4 by a distinct diastema and the presence of two multi-rooted molars with proportions typical of derived multituberculates confirms the cimolodontan affinities of *Corriebaatar*, as first concluded by Rich et al. (2009) on the basis of p4 morphology alone. The dentition of *Corriebaatar* differs from those of non-ferugliotheriid gondwanatherians in possessing a plagiulacoid p4 followed by two molars; non-ferugliotheriid gondwanatherians have four molariform teeth that are not preceded by a plagiulacoid tooth. It also differs from those of euharamiyidans in having a much more robust and more strongly compressed (mediolaterally) lower incisor (which was likely ever-growing), a fully pla-

giulacoid p4 with multiple serrations and no basin, and molars with multiple roots that are not coalesced. Finally, features of the p4 crown (double exodaenodont lobes, long buccal and lingual ridges descending from first serration but extremely short ridges on more distal serrations) are distinctive and diagnostic for *Corriebaatar* relative to other multituberculates, including *Ferugliotherium*.

All available evidence revealed by the two known specimens of *Corriebaatar* confirms that it is a multituberculate firmly nested within Cimolodonta and that, although well separated in time and space, it may be closely related to *Ferugliotherium*.

Biogeographic implications.—Including the holotype specimen of *Corriebaatar marywaltersae* described by Rich et al. (2009), the disputed and undisputed records of multituberculates from the southern supercontinent Gondwana were recently reviewed by Krause et al. (2017). Since that compendium, further doubts have been expressed concerning the original referral of isolated hahnodontid teeth from the Early Cretaceous of Morocco by Sigogneau-Russell (1991) to Multituberculata. Huttenlocker et al. (2018) have argued, in agreement with Butler and Hooker (2005) and Meng et al. (2014), but not with Hahn and Hahn (2006), that the Hahnodontidae are not multituberculates and should be assigned to the Haramiyida, a conclusion that we tentatively accept. Conversely, recent discoveries of dentary fragments of ferugliotheriids from the Upper Cretaceous La Colonia Formation of Argentina support the conclusion that ferugliotheriids are multituberculates rather than gondwanatherians (Brown et al. 2020; for fuller discussion of ferugliotheriid affinities, see Rougier et al. 2021). Multituberculates have also been identified in the Late Cretaceous of Madagascar based on two specimens, a molar fragment (Krause 2013) and a proximal femur (Krause et al. 2017). Finally, Parmar et al. (2013) assigned an isolated tooth, the holotype of *Indobaatar zofiae*, from the Early–Middle Jurassic of India to Multituberculata. These occurrences are depicted in Fig. 7, a paleogeographic map

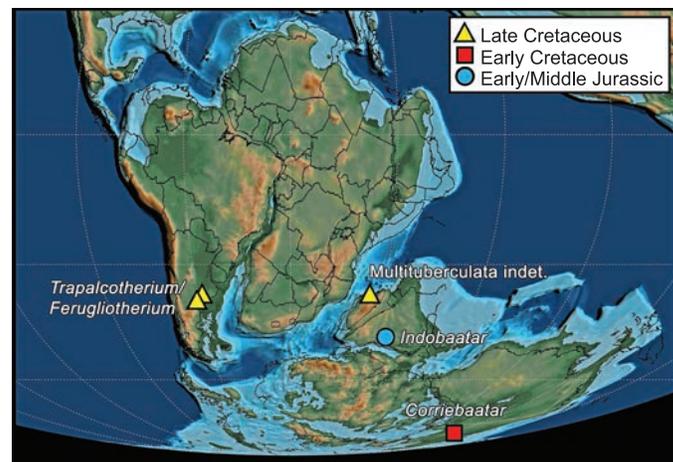


Fig. 7. Known distribution of Mesozoic multituberculates on Gondwana. Base map at 125 m.y.a. (latest Barremian) from Scotese (2021).

of Gondwana in the Barremian (125 Ma; Scotese 2021), the approximate time at which *Corriebaatar* lived.

Given the extremely poor record of Gondwanan multituberculates from the Mesozoic (and the fact that none are known from the Cenozoic), there are profound limitations in formulating testable biogeographic hypotheses. Nonetheless, it must be noted that, if the specimen of *Indobaatar zofiae* from India (Parmar et al. 2013) is verified as that of an eobaatarid multituberculate and its age is verified as Early/Middle Jurassic, its presence informs the possibilities for biogeographic interpretation because it existed at a time prior to the separation of Laurasia and Gondwana and prior to the fragmentation of the latter (Beck 2017).

?*Paracimexomys crossi* Cifelli, 1997 (modified to cf. *P. crossi* by Eaton and Cifelli 2001) is generally accepted as the earliest occurrence of cimolodontan multituberculates (e.g., Cifelli et al. 2014; Weaver et al. 2019). cf. *P. crossi* derives from the Antlers Formation in Oklahoma, which has been dated to near the Aptian/Albian boundary (Jacobs and Winkler 1998; Jacobs et al. 2005), currently regarded as at 113.2 Ma (Gale et al. 2020). Laterally equivalent strata of the Antlers Formation in north-central Texas have also yielded multituberculates, which, although not yet described in detail, also appear to be cimolodontans of the “*Paracimexomys* group” (Krause et al. 1990).

When Rich et al. (2009: 3) described *Corriebaatar marywaltersae* on the basis of only the holotype specimen, they suggested from p4 morphology alone that it was a cimolodontan “as a working hypothesis”. The new, much more complete specimen, NMV P252730, can be taken as strong evidence supporting that hypothesis. The combined evidence from the two specimens, coupled with a revised age for the Flat Rocks site as latest Barremian (Wagstaff et al. 2020), establishes that *C. marywaltersae* is the earliest known cimolodontan. The Barremian/Aptian boundary is currently placed at 121.4 Ma (Gale et al. 2020). Furthermore, *C. marywaltersae*, as a cimolodontan from the latest Barremian of Australia, has additional implications for the origin and early distribution of that group on Gondwana but, given the poor fossil record of multituberculates on the supercontinent (and in the early Mesozoic of Laurasia), we refrain from speculating that its presence indicates an origin for cimolodontans there. Current knowledge, extremely limited by the poor fossil record of early mammalian evolution on Gondwana, allows for multiple scenarios, including both dispersal and vicariance. Nonetheless, *Corriebaatar* establishes that cimolodontans were present on Gondwana during the earlier stages of supercontinental breakup, although separation between West Gondwana (South America and Afro-Arabia) and East Gondwana (Antarctica, Australia, Indian subcontinent, and Madagascar) was already underway (Fig. 7). Of particular note is the highly derived nature of *Corriebaatar* (e.g., absence of p3, morphology of p4), which suggests a ghost lineage for Cimolodonta extending back earlier in time. Furthermore, the presence of multituberculates in the latest Cretaceous of South America and Madagascar could

therefore be viewed as vicariant relicts of an earlier presence on Gondwana. Alternatively, it cannot be discounted (but see Rougier et al. 2021) that the South American record is a result of a later dispersal from North America along with other terrestrial vertebrate taxa during the “First American Biotic Interchange” (Goin et al. 2012; see review in Krause et al. 2019) near the end of the Cretaceous, as suggested by Kielan-Jaworowska et al. (2007).

We eagerly look forward to the recovery of more multituberculate specimens from the Mesozoic of Gondwana to shed further light on their distribution in space and time. Eaton and Cifelli (2001: 454) opined that a “major problem in understanding of multituberculate phylogeny and biogeography is the origin of cimolodontans” and, correspondingly, Kielan-Jaworowska and Hurum (2001: 403) bluntly stated that the origin of Cimolodonta “remains a mystery”; that is still the case over two decades later and is perhaps even more of an enigma in light of the presence of *Corriebaatar* in the mid-Early Cretaceous of Australia.

Authors’ contributions

LK meticulously prepared NMV P252730, AE microCT-scanned the specimen, SM provided the photographs in Fig. 3, PT created the scientific illustrations in Figs. 1 and 5 and provided detailed visual assessments of the specimen that assisted in its description, and MW developed the 3D reconstruction, the 3D PDFs, and the video in SOM. PV-R and THR wrote the original manuscript. Assisted by them, and including contributions from AE and MW to the Material and methods section, DK wrote the second draft.

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